

## The oldest Polyneura (Diptera) and their importance to the phylogeny of the group

Wiesław KRZEMIŃSKI

Accepted for publication: 15 Nov. 1991

KRZEMIŃSKI W. 1992. The oldest Polyneura (Diptera) and their importance to the phylogeny of the group. *Acta zool. cracov.*, 35(1): 45-52.

**Abstract.** The oldest representatives of the families: Tipulidae, Limoniidae, Cylindrotomidae and Trichoceridae are characterized and the relations of the suborder Polyneura to the remaining Diptera are presented and illustrated by dendrograms.

**Key words:** Tipulidae, Limoniidae, Cylindrotomidae, Trichoceridae, fossil, phylogeny.

Wiesław KRZEMIŃSKI, Institute of Systematics & Evolution of Animals, Polish Academy of Sciences, ul. Sławkowska 17, 31-016 Kraków, Poland.

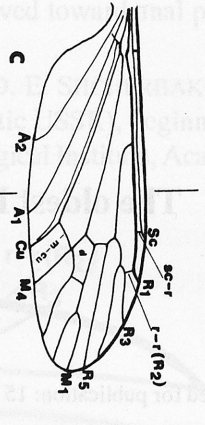
### INTRODUCTION

Since some time the specialists realize that the traditional splitting the Diptera into two groups: Nematocera and Brachycera, however very useful, has no value as far as the phylogenetic relations are concerned. The subject is discussed by HENNIG (1981) and by WOOD and BORKENT in the III volume of the Manual of Nearctic Diptera (1989).

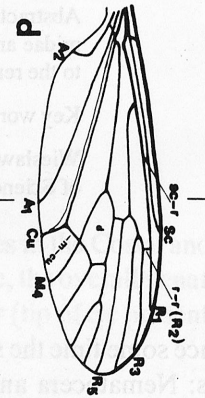
The more natural way is to divide the Diptera into two suborders: Polyneura and Oligoneura. HENNIG (1968, 1981) included to the Polyneura four families: Tipulidae, Limoniidae, Cylindrotomidae and Trichoceridae. The last family was transferred from the Polyneura to the Oligoneura (infraorder Psychodomorpha) by the authors of the Manual of Nearctic Diptera (McALPINE et al. 1981, Vol. I). KRZEMIŃSKI (in press) proposed to divide the Diptera into four suborders: Diarchineura (comprising Tanyderidae and Psychodidae), Neoneura (Eoptychopteridae and Ptychopteridae), Polyneura (sensu HENNIG: Tipulidae, Limoniidae, Cylindrotomidae and Trichoceridae) and Oligoneura (comprising all the remaining families). In the present paper this sense of Polyneura is followed.

I proposed to divide the suborder Polyneura into two infraorders: Tipulomorpha and Trichoceromorpha (Fig. 1). Thus the great similarity of Trichoceridae and Tipulidae adults is stressed and on the other hand - the differences in the larvae are not ignored too. The further division of the Tipulomorpha into 4 families: Limoniidae, Cylindrotomidae, Tipulidae and Pediciidae (raised to the family rank by STARÝ 1992, see this volume) is

TIPULOMORPHA



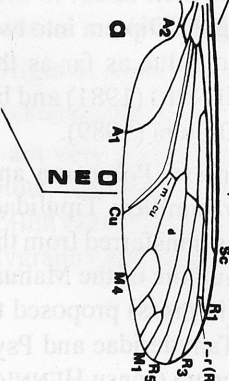
TRICHO CEROMORPHA



POLYNEURA

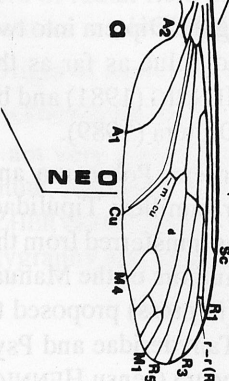


NEURA



OLIGONEURA

NEO



better justified by the real phylogenetic relations among the Tipuloidea than the system promoted by ALEXANDER and BYERS (MND vol. I, 1981) in which all very different members of this superfamily are compressed in one huge family Tipulidae.

## OLDEST FAMILIES REPRESENTATIVES OF THE SUBORDER POLYNEURA.

### a) Limoniidae:

The oldest representative of the suborder Polyneura is a limoniid from the Upper Triassic of North America. Its age is ca. 220 Ma. There were several specimens in a very bad condition, but the main venation characters essential for the determination are retained, especially in one specimen. Also other fragments of the body are preserved. It was described by me as a representative of the genus *Architipula* HANDLIRSCH (Limoniidae) (KRZEMIŃSKI - in press). From the Lower Jurassic on the Limoniidae became very common in the sediments of Europe (Germany, England) (HANDLIRSCH 1906, 1937; TILLYARD 1933, KRZEMIŃSKI and ZESSIN 1990) and Asia (KALUGINA and KOVALEV 1985, ROHDENDORF 1964).

From the Middle Cretaceous on the extinction of Triassic and Jurassic Limoniidae is observed and the new genera (recent genera) appear, as: *Helius* LEPELETIER and SERVILLE, *Limonia* MEIGEN, *Dicranoptycha* OSTEN SACKEN, *Trichoneura* LOEW and another (KRZEMIŃSKI in press; KRZEMIŃSKI and TESKEY 1987; RAYNERS and WATERS 1990). They dominate already from the Paleocene so that it is hard to find a limoniid of that age that would not belong to one of the recent genera.

### b) Trichoceridae:

This is the next family of the Polyneura, represented since Lower Jurassic - German Lias, aged 190 Ma (KRZEMIŃSKI, DAHL and KRZEMIŃSKA - in prep.). The crane flies of this family are generally not frequent in the Jurassic, Cretaceous and Tertiary deposits (KALUGINA and KOVALEV 1985, KALUGINA 1986; DAHL 1971, KRZEMIŃSKI 1985), with the exception for three Asiatic localities, very rich in the Trichoceridae (aged Jurassic/Cretaceous). They represent extinct genera, some of them resembling the recent genus *Nothotrichocera*. There are also very interesting Trichoceridae with long  $A_2$  vein (similar to the recent *Diazosma* BERGROTH; however, true representatives of this genus were found in the deposits not older than Oligocene of North America: SCUDDER 1894). The representatives of the genus *Trichocera* MEIGEN were found in the Baltic amber, Upper Eocene (DAHL 1971; KRZEMIŃSKI 1985).

---

Fig. 1. Phylogenetic tree of the suborder Polyneura and its relation to the suborders: Neoneura and Oligoneura. Wings of: a - representant of fossil family Eoptychopteridae (*Proptychoptera* sp.) Lower Jurassic, Germany; b - representant of recent family Ptychopteridae (*Nasiternella variinervis* (Zett.); c - fossil representant of family Limoniidae (*Architipula* sp.), Lower Jurassic, Siberia; d - fossil representant of family Trichoceridae, Upper Jurassic, Siberia.



### c) Tipulidae:

The first tipulid was found in the deposits not older than the beginning of Upper Cretaceous (ca. 95 Ma, KRZEMIŃSKI 1992, in this volume) - in East Russian, near Vladivostok. I would like to stress that it is the only tipulid found in the period from Triassic to the Tertiary, while there are thousands of Limoniidae and hundreds of Trichoceridae. The family Tipulidae was considered once the oldest, older than the Limoniidae. But the study of fossil specimens leaves no doubt that the Tipulidae is much younger and has numerous apomorphies as compared to the Limoniidae. Tipulidae became more frequent in Paleocene and very common in Eocene, Oligocene and Miocene (HEER 1849; SCUDDER 1894; ALEXANDER 1931; STATZ 1934, 1944; FREIWALD 1990; KRZEMIŃSKI and KRZEMIŃSKA 1990).

Nearly all these specimens fall within the range of variability of the genus *Tipula* LINNÉ. ALEXANDER (1931) classified only one species from Baltic amber to a separate genus *?Electrotipula* ALEXANDER. HEYDEN (1859) recorded a representative of *Ctenophora* from Rott (Upper Oligocene) and GENTILINI (1990) - of the genus *Nephrotoma*. The most species described by SCUDDER, COCKERELL, MEUNIER, TIEOBALD and some another authors need revision.

### d) Cylindrotomidae:

This family has caused a problem to me. ZEUNER (1941) described a cylindrotomid from the Upper Cretaceous of England. I have found this specimen in the Museum of Natural History in London and it appeared to be a limoniid (KRZEMIŃSKI in prep.). So as for now the oldest Cylindrotomidae representant is from the Upper Paleocene/Lower Eocene, Denmark (Andre FREIWALD - personal communication). Its age is about 58 - 55 Ma. The oldest cylindrotomids belong to the extinct genus *Cyttaromyia* SCUDDER and to the recent genus *Cylindrotoma* MACQUART. These genera are also present in Oligocene from North America (SCUDDER 1894) and from East Asia near Vladivostok (FREIWALD and KRZEMIŃSKI, in prep.). The genus *Cyttaromyia* is very interesting, with vein Sc fully retained and terminating in wing margin and additional cross vein r'-m' between R<sub>5</sub> and M<sub>1</sub> present.

## SUMMARY

The importance of fossil materials to the studies on the suborder Polyneura evolution can hardly be overestimated. The trees presented (Fig. 1) are based mostly on the fossil evidences and show how the main lineages of Polyneura had branched off.

At the beginning - probably in Triassic - Polyneura were divided into two infraorders: Trichoceromorpha and Tipulomorpha. A question is what were the ancestors of the entire Polyneura. In my opinion this group cannot be set against the remaining Diptera - so called Oligoneura, which was the idea of HENNIG (1968, 1973, 1981). Probably they evolved from Neoneura, an extinct Triassic group represented by the Eoptychopteridae (KRZEMIŃSKI, in press).

Table I.

The oldest representants of Polyneura and their age (based on the fossils).

CENOZOIC	QUATERNARY		HOLOCENE	1,6		
	TERTIARY	NEOGENE	PLEISTOCENE			
			PLIOCENE	5,3		
			MIOCENE			
		PALEOGENE	OLIGOCENE	23,7		
			EOCENE	36,8		
			PALEOCENE	57,3		
				66,4		
		MESOZOIC	CRETACEOUS		LATE	97,5
					EARLY	
JURASSIC			LATE	144		
			MIDDLE	163		
			EARLY	187		
TRIASSIC			LATE	208		
			MIDDLE	230		
			EARLY	245		
				CYLINDROTOMIDAE		
				TIPULIDAE		
				TRICHOCERIDAE		
				LIMONIIDAE		

CYLINDROTOMIDAE

TIPULIDAE

TRICHOCERIDAE

LIMONIIDAE

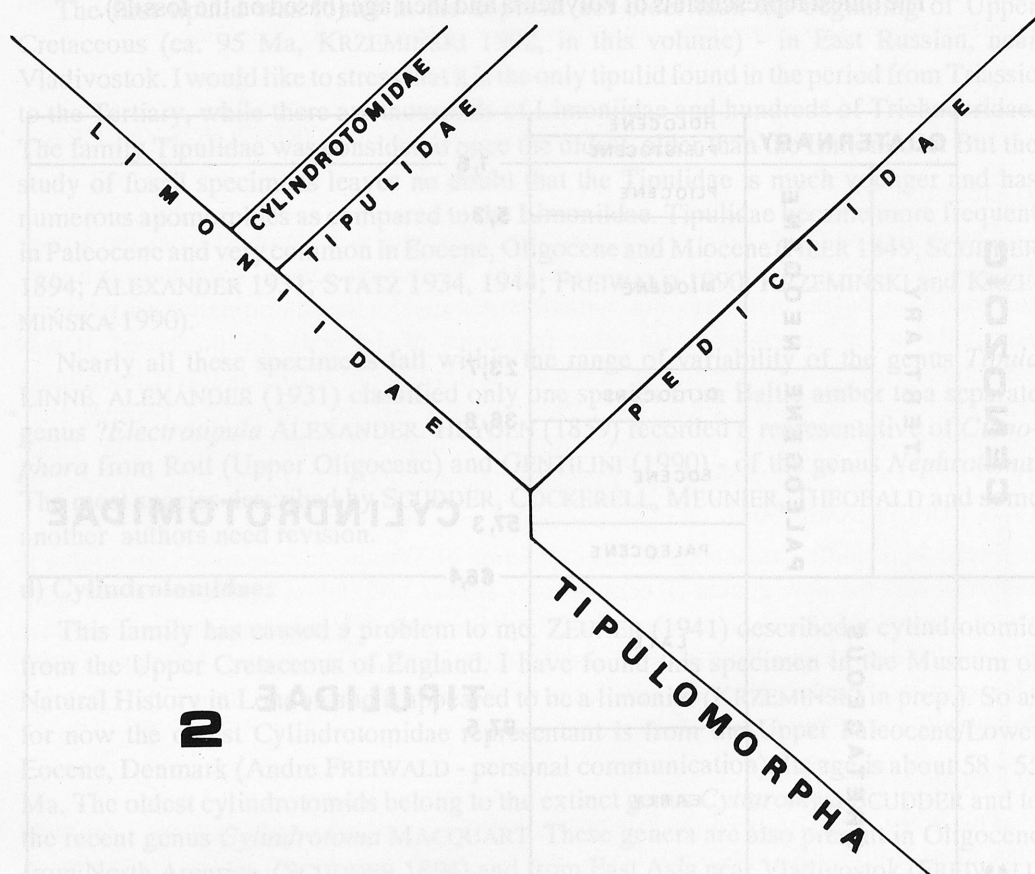


Fig. 2. Phylogenetic tree of the infraorder Tipulomorpha.

Trichoceridae should form a separate infraorder Trichoceromorpha, as KRIVOSHEINA (1988) proposed, but within the Polyneura and not Oligoneura, with single family Trichoceridae. I suppose that the larval characters of Trichoceridae that resemble Psychodidae and Anisopodidae indicate the phylogenetic proximity of these lineages, but cannot counterbalance the characters of the imagines. And these place Trichoceridae in the suborder Polyneura.

Infraorder Tipulomorpha comprises till now Limoniidae, Tipulidae and Cylindrotomidae. I agree with Dr J. STARÝ (1992, see this volume) that the Pediciinae deserve a status of a separate family. To that family Pediciidae I would add some species known since Lower and Middle Jurassic, that till now belonged to other Limoniidae subfamilies. I must admit that I opposed against Dr STARÝ's idea but I had to surrender as the fossil evidences support his conception. Pediciidae has long A<sub>2</sub> vein, apomorphic to the Trichoceridae. On the other hand, these latter have apomorphic radial field, i.e. R<sub>3+4</sub> vein



while some Pediciidae retain plesiomorphic venation of radial field such as the extinct Eoptychopteridae, without  $R_{3+4}$  (Fig. 1a). In this situation apomorphic radial field -  $R_{3+4}$  present - would evolve independently in all these groups: Pediciidae, Limoniidae, Tipulidae and Trichoceridae.

In my opinion family Tipulidae is the sister group to the Limoniidae (Fig. 2) and not to Pediciidae. Their ancestors are among the primitive, extinct Architipulinae. The evidences supporting are: cross-vein m-cu in the fork of  $M_{3+4}$ ; cross-vein sc-r at the tip of Sc and additional character: bare eyes. All evidences prove that Tipulidae is a young family, that had evolved not sooner than in Cretaceous.

Cylindrotomidae are also a very young family, but their phylogenetic position as sister group to Limoniidae or Tipulidae is yet to be clarified.

## REFERENCES

- ALEXANDER C. 1931. Crane-flies of the Baltic Amber (Diptera). Bernstein-Forschungen, **2**: 1-135.
- ALEXANDER C. & BYERS G. 1981. Tipulidae. In: Manual of Nearctic Diptera. Vol. I. Research Branch Agriculture Canada, Monograph **27**: 153-190.
- DAHL C. 1971. Trichoceridae (Diptera) from the Baltic Amber. Ent. Scand., **2**: 29-40.
- FREIWALD A. 1990. Insekten aus der Fur-Formation von Dänemark (Moler, ob. Palaeozän?). 4. Tipulidae. Meyniana, **42**: 47-63.
- GENTILINI G. 1990. Finding of the genus *Nephrotoma* MEIGEN, 1803 from the Upper Miocene of Monte Castellaro (Marche, Central Italy). Boll. Soc. ent. ital., **123**(3): 220-223.
- HANDLIRSCH A. 1906-1908. Die fossilen Insekten und die Phylogenie der rezent Formen. Leipzig, 1-1430.
- HANDLIRSCH A. 1937-1939. Neue Untersuchungen über die fossilen Insekten. II Teil. Ann. Naturhist. Mus. Wien., **49**: 1-240.
- HENNIG W. 1968. Kritische Bemerkungen über den Bau der Flügelwurzel bei den Dipteren und die Frage nach der Monophylie der Nematocera. Stuttg. Beitr. Naturk., **193**: 1-23.
- HENNIG W. 1973. Ordnung Diptera (Zweiflüger). Handb. Zool., 1-337.
- HENNIG W. 1981. Insect phylogeny. Translated and edited by A.C. PONT. JOHN WILEY and Sons, 1-514.
- HEER O. 1849. Die Insektenfauna des Tertiärgesteins von Oeningen und Radoboj in Kroatien. II. Heuschrecken, Flurfliegen, Aderfliegen, Schmetterlinge u. Fliegen. Neue Denkschr. All. Schweiz. Ges. Wissensch., **11**: 1-264.
- HEYDEN C. H. G. 1859. Insekten aus der rheinischen Braunkohle. Palaeontographica, Bd. 8.
- KALUGINA N. & KOVALEV V. 1985. Dvukrylye yuri Sibirii. M., Nauka, 1-198.
- KALUGINA N. 1986. Infraotriady Tipulomorpha i Culicomorpha. In: Nasekomye v rannemelo- vykh ekosistemakh Zapadnoj Mongolii. M., Nauka, 112-115.
- KRIVOSHEINA N.P. 1988. Approaches to solutions of questions of classification of the Diptera. Revue d'Entomologie de l'URSS, **67**(2): 378-389 (In Russian).
- KRZEMIŃSKI W. Triassic and Lower Jurassic stage of Diptera evolution. Mitt. Schweiz. Ent. Ges. - in press.
- KRZEMIŃSKI W. 1985. A representative of Trichoceridae (Diptera Nematocera) from Baltic Amber (in the collection of the Museum of the Earth in Warsaw). Prace Muzeum Ziemi, **37**: 119-121.
- KRZEMIŃSKI W. 1992. *Tipula* (s. lato) *eva* n. sp. from the Cretaceous (East Asia) - the oldest representative of the family Tipulidae (Diptera, Polyneura). Acta zool. cracov., **35**(1): 43-44.
- KRZEMIŃSKI W. & E. KRZEMIŃSKA. 1990. Tipulomorpha (Diptera) of the Middle Eocene deposits from Pesciara di Bolca near Verona (Italy). Acta zool. cracov., **33**(22): 495-499.

- KRZEMIŃSKI W. & H. TESKEY. 1987. New taxa of Limoniidae (Diptera: Nematocera) from Canadian Amber. *Can. Ent.*, **119**: 887-892.
- KRZEMIŃSKI W. & W. ZESSIN. 1990. The Lower Jurassic Limoniidae from Grimmen (Germany) (Diptera Nematocera). *Dtsch. ent. Z., N.F.*, **37**(1): 39-43.
- McALPINE J. F., B. V. PETERSON, G. E. SHIEWELL, H. J. TESKEY, J. R. VOCKEROTH and D. M. WOOD. 1981. *Manual of Nearctic Diptera*, Vol. 1, Research Branch Agriculture Canada, Monograph No. **27**: 1-674.
- RAYNER R. & S. WATERS. 1990. A Cretaceous crane-fly (Diptera: Tipulidae): 93 million years of stasis. *Zool. J. Linn.*, **99**: 309-318.
- ROIDENDORF B. 1964. The historical development of the Diptera. *Trudy paleont. Inst.*, **100**: 1-311. (In Russian. English translation, 1974).
- SCUDDER S. H. 1894. Tertiary Tipulidae with special reference to those of Florissant, Colorado. *Proc. Amer. Phyl. Soc.*, **32**: 163-245.
- STARÝ J. 1992. Phylogeny and classification of Tipulomorpha, with special emphasis on the family Limoniidae. *Acta zool. cracov.*, **35**(1): 11-36.
- STATZ G. 1934. Neue Tipulidenfunde aus den Braunkohlen-schiefern von Rott am Siebengebirge. *Wissenschaft. Mitteilgn. d. Ver. f. Nat. u. Heimatk.*, Köln, **1**(3): 22-38.
- STATZ G. 1944. Neue Dipteren (Nematocera) aus dem Oberoligozän von Rott. III. Familie Limnobiidae (Steltzmücken). *Palaeontographica*, Stuttgart, Bd. 45, Abt. A.: 94-191.
- TILLYARD R. J. 1933. The panorpoid complex in the British Rhaetic and Lias. *Fossil Insects*, London (Brit. Mus. Nat. Hist.), **3**: 1-78.
- WOOD D. M. and A. BORKENT. 1989. Phylogeny and classification of the Nematocera. In: *Manual of Nearctic Diptera*. Vol. 3. Research Branch Agriculture Canada, Monograph No. **32**: 1333-1366.
- ZEUNER F. E. 1941. The Eocene insects of the Arden Beds, Isle of Mull, Scotland. *Annals and Magazine of Natural History*, **11**(7): 82-97.